

COSTS AND BENEFITS OF FORAGING ASSOCIATED WITH DELAYED DISPERSAL IN THE SPIDER *ANELOSIMUS STUDIOUS* (ARANEAE, THERIDIIDAE)

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ABSTRACT. In the theridiid spider, *Anelosimus studiosus*, most juveniles remain in their natal web, forming temporary colonies in which individuals cooperate in web maintenance and prey capture until they disperse at maturity. There is natural variation in age at dispersal, and subadult spiders removed from their natal webs build webs and continue to develop. To explore the costs and benefits of delayed dispersal, we compared the rate of prey capture and developmental rate for individuals in colonies and those isolated at the fourth instar. Rate of prey capture by colonies increased with colony size and age; this result was driven primarily by the enhanced capture of large prey by larger and older colonies. The presence of juveniles increased the overall productivity of webs, an effect which remained after the juveniles were removed from the web. Despite the overall increase in prey capture, per-individual prey capture decreased with colony size. The variance in prey capture success decreased significantly with colony size, but not with colony age. Spiders in colonies captured more prey per juvenile than singletons experimentally dispersed at the fourth instar; however, this did not result in increased development rate of colonial juveniles over isolated juveniles. These data suggest that juvenile *A. studiosus* benefit from delayed dispersal by acquiring more resources and acquiring them more steadily. The productivity of webs of females whose juveniles were removed at the fourth instar remained higher than those of similarly aged females who never produced juveniles. This suggests that delayed dispersal of juveniles enhances the resources which the female could allocate to her next egg mass.

Keywords: Parental investment, sub-sociality, risk-sensitivity, cooperative foraging

Because spiders are generally limited by resources (Wise 1993), it is likely that any resources a mother spider provides to her juveniles would reduce her future egg production. Thus the behavior of maternal social spiders would fit Trivers' (1972) definition of parental investment, in which a mother's behavior enhances the survival of her current brood, at a cost to her production of future broods. However, if juveniles remain in their natal webs beyond an early altricial phase and become active in the web, their continued presence may enhance prey capture and/or defense. This in turn could enhance the mother's production of future broods. In this way a mother may recoup her initial parental investment in terms of future reproductive success. The objective of this work is to describe the relative costs and benefits of delayed dispersal in *Anelosimus studiosus* (Hentz 1850), a spider in which the maternal-juvenile association is longer than in most maternal social species. We used laboratory ex-

periments to examine the effects of delayed dispersal on prey capture and development rate of late instar juveniles. We also examined the post-dispersal prey capture of webs in order to determine if delayed juvenile dispersal could enhance a mother's future reproductive success.

The effect of maternal care on the survival and growth of juveniles in maternal social spiders is well documented. Guarding of egg sacs is a relatively common form of maternal care in spiders, providing protection from predation and parasitism (Foelix 1996). In colonies of the theridiid spider *Theridion pictum* (Walckenaer 1802), unguarded egg sacs had drastically reduced hatching success, but juvenile size was not affected (Ruttan 1991). In about 20 described species, mothers actively provision their offspring with paralyzed or regurgitated prey (Foelix 1996). Mothers of the European agelenid spider *Coelotes terrestris* (Wider 1834) provision their offspring and protect them from predators and parasites un-

til the juveniles disperse after about one month (Horel & Gundermann 1992). Under laboratory conditions, the mother's presence had a significant positive effect on juvenile survival. The mother's parental investment, in terms of her ability to produce a second brood, was small relative to the enhanced survivorship of the current brood (Gundermann et al. 1997).

The 17 known species of non-territorial permanent-social spiders represent six families and are mostly found in the tropics (Avilés 1997). Several studies have indicated that individual survivorship of colony members is greater than that of solitary individuals (Christenson 1984; Riechert 1985; Avilés & Tufiño 1998). Potential benefits of group living for spiders include reduced individual silk costs (Riechert et al. 1985; Tietjen 1986), capturing larger prey (Nentwig 1985; Rypstra 1990; Rypstra & Tiley 1990; Pasquet & Krafft 1992) and reduced predation (Henschel 1998). Fecundity in social spiders is lower than in solitary species (Riechert 1985; Vollrath 1986; Wickler & Siebt 1993). Female *Anelosimus eximius* in large colonies have lower fecundity than those in intermediate colonies (Keyserling 1884, Avilés & Tufiño 1998). Potential costs of sociality for spiders include competition within the group (Rypstra 1993), increased incidence of parasitism (Avilés & Tufiño 1998), and susceptibility to diseases (Henschel 1998).

The social behavior of the theridiid spider, *A. studiosus*, is intermediate between the maternal social and the non-territorial permanent-social spiders (Brach 1977), and the costs and benefits of delayed juvenile dispersal may go beyond simple parental investment. If web productivity is sufficiently enhanced by the presence of the late-instar, participating juveniles, this enhancement could balance the costs of parental care to the mother, or even enhance her production of future broods. In this regard, *A. studiosus* may represent an evolutionary intermediate between maternal social and non-territorial permanent-social spiders and, thus, could provide an important link in understanding the evolution of spider sociality.

METHODS

Study species.—*Anelosimus studiosus* range from Argentina to New England and are

typically found in open habitat, building webs at the tips of branches in low shrubs (Brach 1977). Adult females are fertilized before leaving the natal web or shortly after dispersal. The mother produces and guards an egg case, feeds newly-emerged offspring through regurgitation, and provides second instar juveniles with paralyzed prey. As the juveniles develop beyond the second instar, they participate increasingly in prey capture and web maintenance (Brach 1977). Juveniles isolated at the fourth instar or later can build their own webs, capture prey and continue to develop (Brach 1977; pers. obs.). Males are mature at the sixth post-emergent instar, and females at the seventh (pers. obs.). As the juvenile females mature, the mother becomes aggressive towards them, forcing them from the web (Brach 1977; but see Furey 1998). Adult males are always tolerated in the web by the mother; therefore, the maturing males apparently disperse of their own accord (Brach 1977). Female *A. studiosus* can produce up to three consecutive broods using the same web (pers. obs.).

Rearing methods.—We collected 16 colonies from the Ocala National Forest in Florida in 1994 and 1995. We reared these colonies on live shrubbery within a 3.6 m × 2.4 m × 2.1 m enclosure in the Biological Sciences Greenhouses located at The Ohio State University, maintained at temperatures between 23–32 °C, with a combination of natural light and supplemented light (on cloudy days) reflecting the natural light cycle. Flying prey (*Musca domestica*, *Drosophila melanogaster* and *D. hydei*) were released into the enclosure three times a week, at which time the colonies were misted with distilled water. From the enclosure, we collected 72 adult females dwelling singly in newly-constructed webs in late March and early April 1997 and maintained them individually in 500 ml plastic containers. Each spider was provided a coiled twist-tie, which they used as a retreat. We fed them *ad libitum*, misted them three times a week, and exposed them to a male for 24 h within the week after they were collected. Voucher specimens are placed in The Museum of Biological Diversity at The Ohio State University.

Experimental procedure.—Thirty-eight of the 72 isolated females produced egg cases. We placed these, with their egg sacs and retreats, onto a small piece of artificial shrub-

bery for 24 h while they constructed new webs. We then wired these new webs into the middle of larger arrangements of artificial shrubbery which were standardized by number, size and positioning of the leaves. We housed the webs, individually, within cuboidal enclosures 46 cm on a side (these were screened on the four sides and solid on the top and bottom). Three times a week, we misted the webs and released two *M. domestica* and ten *D. melanogaster* into the enclosure. We censused each web 48 h after prey release for the numbers and types of prey captured, as well as the numbers and age classes of juveniles present in the web. We removed the carcasses of captured prey from the webs and enclosures after each census.

We assigned webs to two groups. In the treatment group we removed the juveniles from their natal web when the majority of them had reached the fourth instar, and individually placed three of the juveniles as singletons into the experimental conditions described above. In the control group we removed the juveniles similarly, but immediately replaced them and allowed them to develop and disperse naturally. We assigned webs to the two groups by first ranking them in order of number of juveniles in the web, then flipping a coin to decide the treatment of the first web, alternating the assignment of the remaining webs thereafter. We did this to ensure a fair representation of the range in number of juveniles in each treatment. There was no juvenile mortality or dispersal over the period for which the results are reported; thus, the number of juveniles remained constant within colonies.

Seventeen females without juveniles were maintained under the experimental conditions for comparison with webs of similar age containing juveniles. Of these, ten did not produce egg sacs, and seven produced egg sacs that did not hatch. If any of the adult females died during or within a week after the experimental period, we did not include data from their webs in the analyses. Twenty of the 38 egg sacs produced did not hatch, and six of the mothers died during the experiment. Data from seven control webs and five experimentally-dispersed webs were used.

We estimated the amount of extractable resources for a given prey type as the average wet weight minus its average dry weight (13.1

mg for houseflies, 0.4 mg for *Drosophila*). Prey capture success was recorded as the number of each prey type times their extractable weight. Due to asynchronous juvenile development, the age class of a web was described by the instar of the majority of the juveniles in it.

Data analysis.—In analyses exploring how colony size affects the amount of prey captured, we calculated the mean per-trial prey capture over the period that juveniles were present. We estimated the per-juvenile prey capture by dividing the total mass of prey captured in a trial by the number of juveniles in the colony. To analyze how colony size affects variation in prey capture, we used the coefficient of variation (CV) among trials within colonies, in per-juvenile prey capture. We chose CV to standardize for the fact that we expect the variance to increase as the mean increases. We used regression analyses on the means and CVs of the colonies to test for effects of colony size. In analyses of effects of colony age on foraging success we used data from the colonies multiple times (means and CVs at each instar within colonies), resulting in non-independence of the data. To account for this, we performed repeated measures analyses of covariance, with the instar of the majority of the juveniles as the covariate, and the individual colony as a random factor.

RESULTS

Effects of delayed dispersal on prey capture.—Across all webs, prey capture increased significantly with juvenile age (Fig. 1). In this plot, data from both the treatment and control colonies are factored into the means of the first three instars, because at that point both sets were intact and undisturbed. Only the control colonies are factored into the means of fourth through sixth instars. However, we used only data from the control colonies in the repeated measures ANCOVA. Mean per-trial prey capture also increased significantly with number of juveniles in the colony (Fig. 2). Despite the overall increased productivity of larger webs, there was less prey available to individual spiderlings as the number of juveniles increased (Fig. 3). The average coefficient of variation in per-juvenile prey capture showed no trend with respect to colony age (Fig. 4). There was, however, a significant decrease in the coefficient of vari-

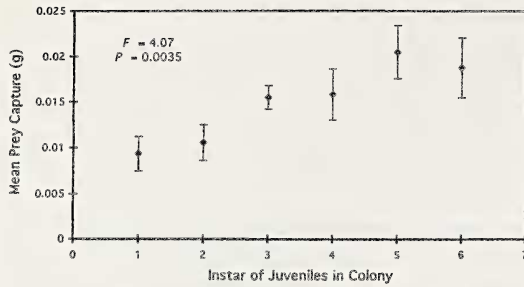


Figure 1.—Average per-trial prey capture during the period juveniles were in the web vs stage of the colony. Plotted are the means for the colonies at a given instar with standard error bars (repeated measures ANCOVA $F = 4.07$, $P = 0.0035$).

ation in per-juvenile prey capture as colony size increased (Fig. 5).

Much of the effects of colony size and age on foraging success were driven by the enhanced ability of larger and more mature colonies to capture the larger prey items. The average number of houseflies captured per trial increased significantly with colony size ($R^2 = 0.79$, $P = 0.007$; regression of the average number of houseflies captured per trial on the log of the number of juveniles in the colony). This increase was non-linear and asymptotic because the larger colonies depleted the available flies. There was also a significant increase in the mean number of houseflies captured with colony age ($F = 2.69$, $P = 0.04$; repeated measures ANCOVA with juvenile instar as a cofactor).

Effects of delayed dispersal on juvenile development.—The development rate of juveniles in colonies, as measured by the amount of time required to reach the fourth or

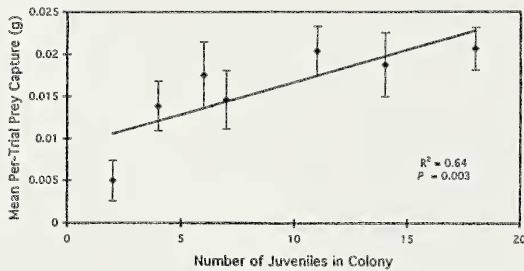


Figure 2.—Average per trial prey capture during the period juveniles were in the web vs number of juveniles in the colony. Plotted are the means for each colony over all instars with standard error bars ($R^2 = 0.64$, $P = 0.003$).

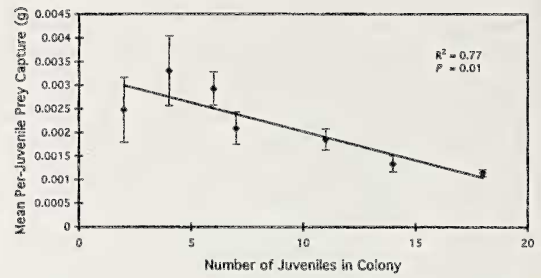


Figure 3.—Average per-juvenile, per-trial, prey capture during the period juveniles were in the web vs number of juveniles in the web. Plotted are the means for each colony over all instars with standard error bars ($R^2 = 0.77$, $P = 0.01$).

sixth instars, was not related to prey capture per juvenile (Fig. 6). Similarly, when these development rates were compared to the coefficients of variation in per-juvenile prey capture success, no trends were found (Fig. 7).

Experimentally dispersed fifth instar singletons captured fewer prey, on average, than the per-juvenile rate for a colony (Mann-Whitney $U = 56.0$, $P < 0.01$; Fig. 8A). The main cause of this difference was the fact that the singletons captured only *Drosophila* while the colonies were able to capture houseflies. The difference in prey capture did not result in a difference in development rate, as measured by the duration of the fifth instar, between colony juveniles and singletons (Mann-Whitney $U = 37.0$, $P = 0.92$; Fig. 8C). Male singletons captured significantly less prey (Mann-Whitney $U = 114.5$, $P = 0.002$), and developed significantly more slowly in the fifth instar

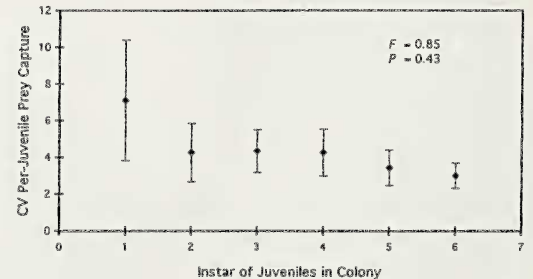


Figure 4.—Coefficient of variation in per-juvenile prey capture within instar, within colonies, vs stage of the colony. Plotted are the mean variances of the colonies at each instar with standard error bars (repeated measures ANCOVA $F = 0.85$, $P = 0.81$).

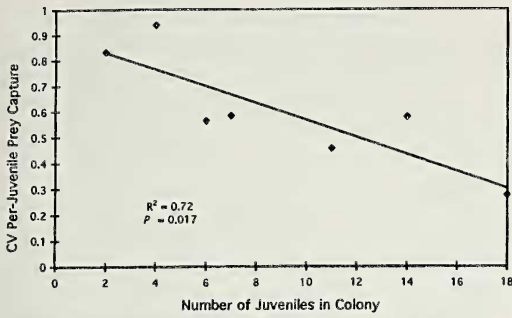


Figure 5.—Coefficient of variation in per-juvenile prey capture, within colonies, vs number of juveniles in the colony. Plotted are the variances for each colony pooled over all instars ($R^2 = 0.72$, $P = 0.017$).

(Mann-Whitney $U = 49.0$, $P = 0.002$), than female singletons (Figs. 8B, 8D).

Effects of delayed dispersal on a mother's future reproductive success.—To examine potential foraging benefits to the mother associated with delayed dispersal of her offspring, we compared prey capture within and among the webs of females which did not produce egg cases (Group A, Table 1), webs in which females were guarding egg cases that did not hatch (Group B, Table 1), and the webs from which the juveniles had been experimentally dispersed (Group C, Table 1). There were no differences in prey capture in the first week between any of the categories of webs, nor were the webs in which there were no juveniles more productive in the 5th week than they were at the first. Females who had had juveniles in their webs captured significantly more prey during the week after their offspring were dispersed (which on average was around the fourth week after being placed on the plant) than did either of the two categories that had not had juveniles. Prey capture of females the week after their juveniles were removed was not different than that of the week prior while the juveniles were still present.

DISCUSSION

The results presented here demonstrate that the presence of juveniles increased the overall productivity of webs, and that productivity increases with both the age (Fig. 1) and the number of juveniles in the web (Fig. 2). The majority of these effects were driven by the ability of larger and older colonies to capture

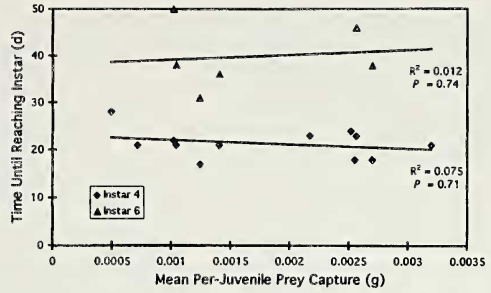


Figure 6.—Colonial juvenile development vs mean per-juvenile prey capture. The points plotted are the times taken by colonies to reach the specified instar (4th instar, $R^2 = 0.012$, $P = 0.74$.; 6th instar $R^2 = 0.075$, $P = 0.71$).

more houseflies, one of which has more extractable resources than all ten of the *Drosophila* combined. These results are consistent with those found for several permanent-social spider species (Riechert et al. 1986; Tietjen 1986) including a congener of this species, *A. eximius* (Nentwig 1985; Rypstra 1990), as well as in colonial orb-weaving spiders (Uetz 1989). In these studies, social spiders captured larger prey and a wider range of prey sizes than solitary spiders of similar size.

There was a significant decrease in the coefficient of variation in per-juvenile prey capture associated with the number of juveniles in the colony (Fig. 5). Reduced variance in foraging success has been identified as a potential benefit of spider coloniality in a dynamic model (Caraco et al. 1995), and in colonial orb-weaving *Metepeira* spp. (Uetz 1988a, 1988b). These studies found that, under high prey densities, coloniality represents

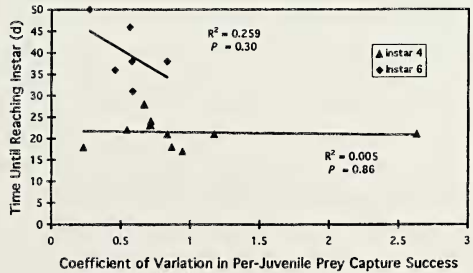


Figure 7.—Colonial juvenile development vs mean coefficient of variation in per-juvenile prey capture. The points plotted are the times taken by colonies to reach the specified instar (4th instar, $R^2 = 0.259$, $P = 0.30$; 6th instar $R^2 = 0.005$, $P = 0.86$).

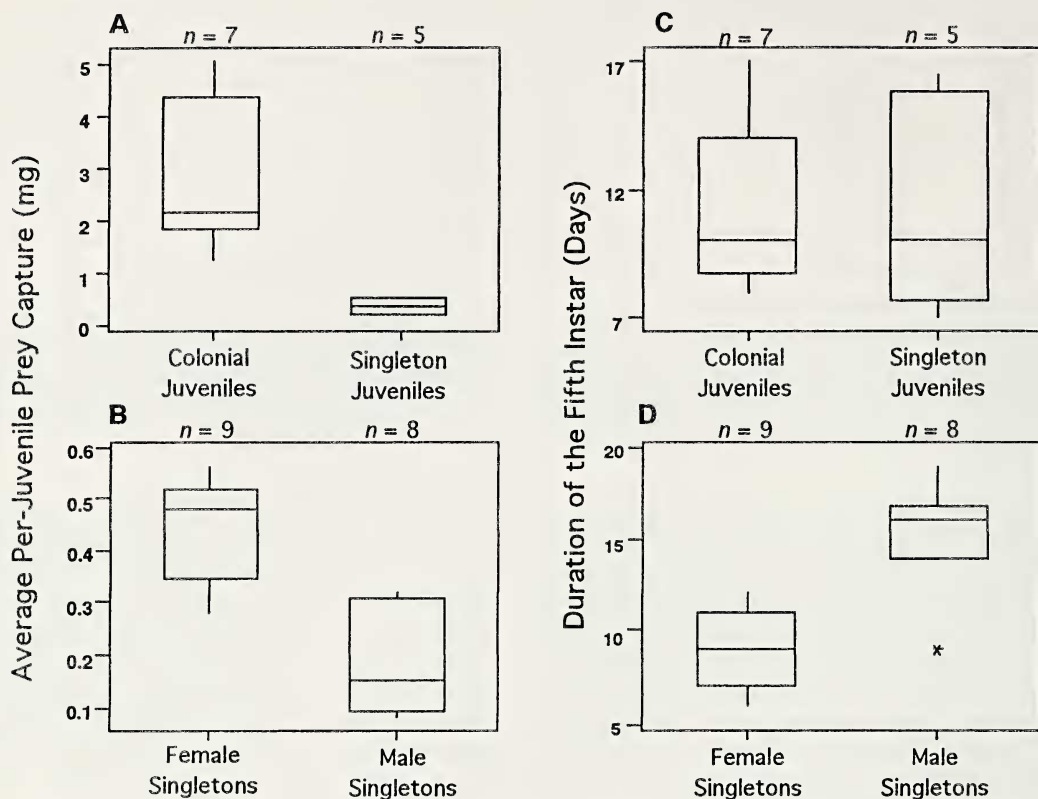


Figure 8.—Boxplots comparing prey capture and juvenile development between colonial and singleton juveniles. Plotted are the medians, inter-quartile ranges and standard ranges (see text for significance statistics).

a 'risk averse' strategy in which the spiders trade a reduction in mean individual capture rate for a reduction in variance in capture rate.

We found no relationships between mean or CV in per-juvenile prey capture and development rate (Figs. 6, 7), nor did the singleton juveniles develop more slowly than colonial individuals, despite the greatly-reduced prey capture in singletons (Fig. 8C). This suggests that, under these prey densities, the colonies were capturing considerably more prey than they could physiologically assimilate.

Female singletons were more successful at capturing prey than male singletons (Fig. 9B). Though not measured directly, the female singletons' webs appeared larger and denser than those of the males. Among the non-territorial permanently-social spiders, males typically do not participate in web activities, and in such species the adult sex ratios are skewed towards females (Avilés 1997). These skewed sex ratios have apparently evolved through

group selection, meeting the stringent conditions required to select for a trait which is beneficial to the colony but which, within the colony, reduces the fitness of individuals possessing it (Avilés 1986, 1993; Smith & Hagen 1996). The data presented here suggest that female *A. studiosus* may benefit by skewing their broods toward females. If web productivity increases with the proportion of female juveniles, there may be an optimal brood sex ratio which balances the increased survivorship of female-biased broods, with Fisher's (1958) selective pressure towards an equal investment between male and female offspring. A female biased sex ratio was reported for this species in a Tennessee population (Furey 1998), but was not found among specimens from Ecuador (Avilés & Maddison 1991).

The results presented here suggest that *A. studiosus* juveniles benefit from remaining in their natal web by obtaining more resources, and more consistent resources, than they

Table 1.—Weekly web productivity averages, variances and specific comparisons (*T* statistics and *P* values) for three types of web. Group A females did not produce egg sacs, Group B females produced egg cases which did not hatch, and Group C females produced egg cases which hatched, and had their juveniles removed at the fourth instar.

Week	Group A No egg sac produced (<i>n</i> = 8)		Group B Eggs did not hatch (<i>n</i> = 6)		Group C Juveniles removed at 4th instar (<i>n</i> = 5)		
	Wk 1	Wk 5	Wk 1	Wk 5	Wk 1	Wk 4	Wk 5
Mean (g)	0.0017	0.0033	0.0014	0.0034	0.0032	0.0156	0.0150
Variance	3.6 E-6	4.0 E-6	4.5 E-6	6.1 E-6	1.2 E-5	1.3 E-5	5.4 E-5
A (wk 1)	—	-1.63	0.26		-1.04		
		<i>P</i> = 0.073	<i>P</i> = 0.40		<i>P</i> = 0.16		
A (wk 5)		—		-0.021			-8.0
				<i>P</i> = 0.49			<i>P</i> = 3 E-6
B (wk 1)			—	-1.28	-1.07		
				<i>P</i> = 0.13	<i>P</i> = 0.156		
B (wk 5)				—			-6.69
							<i>P</i> = 5 E-5
C (wk 1)					—		-10.2
							<i>P</i> = 0.0003
C (wk 4)						—	-0.18
							<i>P</i> = 0.43
C (wk 5)							—

would as singletons. However, because per-individual prey capture decreases with colony size (Fig. 3), for any given prey density there will be an upper limit to the number of juveniles a colony can support. Colony sizes in this experiment were lower than those reported for natural colonies (a mean of 36 juveniles at hatching; Brach (1977)).

While the potential benefits of delayed dispersal to the juveniles are relatively clear, there is indirect evidence that there are benefits to the mother as well. In this study, females in webs that previously had juveniles captured more prey than those with webs of the same age that had not (Table 1), but webs that had had juveniles were no less productive during the week after the juveniles were removed than during the previous week with the juveniles present. This suggests that the juveniles' main contribution to web productivity is in web construction rather than in subduing prey. While size of webs was not measured, webs with juveniles present became noticeably larger than webs without.

Because there is no observed aggression between a mother and her younger offspring, or among juveniles (Brach 1977), it is likely that captured prey is divided evenly (or at

least randomly) among colony members. Observations of interactions among colony members are limited for this species, and it is possible for the mother or larger juveniles to dominate captured prey. Further work is needed to explore potential sibling rivalries and parent-offspring conflicts in this species.

It should be kept in mind that, in this experiment, prey densities were artificial, standardized, and depletable. Prey densities were chosen in an attempt to eliminate nutritionally related mortality, not to represent natural conditions. Therefore, the extent to which the protocol reflects conditions associated with the evolutionary maintenance of *A. studiosus* behavior is limited; however, the internal comparisons of the experiment remain robust. The depletion of the prey in a given trial puts an upper limit on possible prey capture success (although in only two trials did a web capture all of the prey released). Prey density during a trial decreased as prey were captured, resulting in a decline in the probability of capturing more prey. Overall, prey depletion should have the effect of reducing the power of the experiment to detect factors that affect the mean capture rate of webs; prey depletion may also create a spurious reduction in vari-

ance measures as the more productive webs approach prey depletion.

That neither colonial nor singleton juveniles appeared to be food-limited in this study is suggested by the stable growth rates of juveniles regardless of group size or prey capture rate. These results would predict that under lower prey densities food limitation would affect the singleton juveniles more than colonials, except when the colony is so large that the per-juvenile prey capture is below that of singletons. As long as prey densities are high enough on average to support the colonies, the reduction in variance associated with cooperative foraging may allow the juveniles to assimilate the resources more efficiently.

The data presented here suggest that delayed dispersal of a brood could enhance the mother's production of future broods by increasing the productivity of her web. The experimental conditions were relatively mild, compared to natural conditions where webs are frequently damaged, particularly by rainfall. Thus, cooperative web maintenance in this species may be even more important than this study would suggest.

From these experimental data, it seems likely that cooperative foraging plays a significant role in the evolutionary maintenance of delayed offspring dispersal in *Anelosimus studiosus*. While this work has identified several potential advantages of delayed dispersal, the specific nature of the costs and benefits would need to be tested under more natural conditions. This is also true for other factors which could influence the maintenance of delayed dispersal such as predation risk and parasitism.

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